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PLANT COMMUNITY PATTERNS IN UNBURNED AND BURNED BLACKBRUSH (*COLEOGYNE RAMOSISSIMA* TORR.) SHRUBLANDS IN THE MOJAVE DESERT

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ABSTRACT.—The blackbrush vegetation type is dominated by *Coleogyne ramossisima*, which is thought to preclude the coexistence of many other plant species. Fire can remove blackbrush cover and possibly increase plant species richness and evenness. Fire also may increase the frequency and cover of alien annual grasses, thereby intensifying landscape flammability. We tested these predictions in unburned and burned (6–14 years postfire) blackbrush at 3 sites spanning the range of this vegetation type in the Mojave Desert.

Species richness in unburned blackbrush was similar to published values for other vegetation types in western North America, but richness varied significantly among the 3 sites and 4 spatial scales (1, 10, 100, and 1000 m^2). Richness values declined in order from annual forbs, woody perennials, herbaceous perennials, annual grasses, cacti, to perennial grasses. Fire reduced *Coleogyne* cover, thus boosting species evenness. In contrast, species richness decreased after burning, although the results varied among spatial scales. Total cover was unaffected by fire because cover of woody perennials decreased, while cover of annual forbs, annual grasses, herbaceous perennials, and perennial grasses increased. Native species richness and cover decreased, whereas alien richness and cover increased after burning, especially where the alien forb *Erodium cicutarium* was present. Fire had no effect on frequency and variable effects on cover of alien annual grasses. These results indicate that in blackbrush species richness can vary among sites and local spatial scales, and effects of fire can vary among plant life-forms and between natives and aliens.

Key words: blackbrush, Coleogyne ramosissima, *fire, alien plants, plant species diversity, Mojave Desert.*

The blackbrush vegetation type occurs at the bioregional transition between the Mojave and Great Basin Deserts, from California through Nevada, Arizona, and Utah (Bowns 1973). In the Mojave Desert blackbrush occupies the elevational zone from approximately 1220 m to 1525 m, above the zone dominated by creosote bush (*Larrea tridenata*) and below the zone dominated by sagebrush (*Artemisia* spp.; Bradley and Deacon 1967, Randall 1972, Beatley 1976). Blackbrush is dominated by the type species, *Coleogyne ramosissima,* which can comprise 90–95% of total plant cover (Shreve 1942). For clarity in this paper, we refer to the vegetation type as blackbrush and the type species as *Coleogyne.*

Although 185 species of vascular plants have been found growing within blackbrush (Vasek and Barbour 1988), they are never very abundant except at upper- and lower-elevational ecotones (Bowns 1973, Beatley 1976, West and Young 2000). Beatley (1976) stated that "so nearly complete is the dominance of this shrub species that in areas that are not ecotonal there are only a few associated shrub species, and these occur usually as scattered plants in an otherwise pure stand of *Coleogyne.*" Thus, species richness and evenness of vascular plants is generally thought to be low in blackbrush compared with other vegetation types in western North Amercia.

Most accounts describing the dominance of *Coleogyne* in blackbrush indirectly suggest that high cover of this species results in the competitive exclusion of other plant species (Bowns 1973, Beatley 1976, Bowns and West 1976). If this is true, then reduction of *Coleogyne* cover should lead to heightened species richness and evenness. Fire has been used to reduce *Coleogyne* cover and promote the growth of more palatable rangeland species (Bowns 1973), but the effects of fire on plant species diversity are unknown.

Effects of fire on blackbrush appear to be long term. There is only 1 report of *Coleogyne* resprouting after fire (Bates 1984), 2 reports of seedling establishment by *Coleogyne* after fire (Ellison 1950, Lei 1999), and 1 report of

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autogenic succession back to blackbrush after fire (Thatcher 1975). In the latter case, fire intensity was likely very low and *Coleogyne* survival very high, resulting in incomplete removal of *Coleogyne,* which allowed the direct reestablishment of the blackbrush vegetation type. Most studies report that blackbrush does not reestablish after fire (Bowns 1973, Beatley 1976, West and Young 2000), even 37 years postfire (Callison et al. 1985). A wide range of species can dominate after *Coleogyne* is removed by fire (Jenson et al. 1960, Bowns 1973, Wright and Bailey 1982, Bates 1984, Callison et al. 1985). Annuals typically dominate during the first few postfire years, and early successional perennial plants dominate after the first few decades (Jenson et al. 1960, Bates 1984, Callison et al. 1985). Although the species composition can be highly variable (Bowns 1973), the alien annual grasses red brome (*Bromus madritensis* ssp. *rubens*) and cheatgrass (*Bromus tectorum*) are often among the most common postfire species (Jenson et al. 1960, West 1983, Callison et al. 1985).

Alien annual grasses can create a continuous cover of fine fuel that persists for years, thereby facilitating the spread of fire in the Mojave Desert (Brooks 1999). Recurrent fire may increase the cover and frequency of alien annual grasses (Whisenant 1990, D'Antonio and Vitousek 1992), promoting additional fires and possibly replacing long-lived native species in the Mojave Desert (Brooks and Esque 2000, Brooks 2003). Slow recruitment rates of *Coleogyne* should make this species particularly sensitive to the effects of recurrent fire. Although blackbrush produces the highest cover of all native vegetation types in the Mojave Desert (up to 51%; Beatley 1975), which is partly why it is considered the most flammable (Bowns 1973, Beatley 1976, West 1983), high cover and frequency of alien annual grasses may create even more flammable fuel conditions (Holmgren 1960).

In this study we report plant community characteristics of higher vascular plants (seed plants) in unburned and burned blackbrush in the Mojave Desert. We predicted that species richness in blackbrush would be lower than that reported for other vegetation types in southwestern North America, and that fire would increase species richness and evenness by removing *Coleogyne.* We also predicted that fire would increase cover and frequency of alien annual plants, grass species in particular.

STUDY AREA

Three study sites were established from the northeast to the southwest Mojave Desert, in the middle of the blackbrush zone between the upper and lower ecotones in each region. The Beaver Dam site (37°11′17″N, 113°56′39″W, 1230 m) is in the Bureau of Land Management, St. George Field Office region of southwestern Utah. The Spring Mountain site (36°01′40″N, 115°3′10″W, 1470 m) is in the Spring Mountain National Recreation Area of the Humboldt-Toiyabe National Forest in southern Nevada. The Joshua Tree site (34°03′23″N, 116°19′45″W, 1370 m) is located at Joshua Tree National Park in southern California.

Soils at the Beaver Dam site are classified as Cave gravelly sandy loams, which occur on dissected, old, coalescing alluvial fans or bajadas, with a petrocalcic horizon ranging from 20 cm to 51 cm below the surface (Mortensen et al. 1977). Parent materials are mixed gravelly alluvium from weathered gneiss, limestone, dolomite, quartzite, shale, and acid igneous rocks. The Spring Mountain site soils are a combination of Purob and Irongold extremely gravelly loams, which occur on alluvial fan remnants, with depths to a petrocalcic horizon ranging from 36 cm to 51 cm (Douglas Merkler, Natural Resources Conservation Service, personal communication). These soils were formed in alluvium mainly derived from limestone. Soils at the Joshua Tree location are sandy loams derived from alluvial granitic parent materials, with no apparent petrocalcic horizons near the surface (MLB personal observation). All study plots were established on level to slightly sloping surfaces.

Each site consisted of mature blackbrush and an adjacent burned area located on similar soils and topography. Burned areas were created by a wildfire in 1995 at the Beaver Dam site, a wildfire in 1987 at the Spring Mountain site, and a prescribed fire in 1993 at the Joshua Tree site.

METHODS

The 3 sites were sampled in spring 2001, during the phenological peak for annual plant biomass, and 6, 8, and 14 years postfire at the Beaver Dam, Joshua Tree, and Spring Mountain sites, respectively. At each site we established eight 4-ha plots, 4 in unburned blackbrush and 4 in previously burned blackbrush. These plots were established for another study designed to evaluate the effects of 4 fuel management treatments during 2002 (spring burning, summer burning, herbicide or mechanical treatment, and untreated control). Results of these treatments will be reported elsewhere.

Within each 4-ha plot we established 2 modified-Whittaker sampling plots (Stohlgren et al. 1995). Each sampling plot was 20 × 50 m (1000 m^2), with one 5 × 20-m (100 m^2) subplot, two 2 × 5-m (10 m^2) subplots, and ten 0.5 × 2-m (1 m^2) subplots. Canopy cover of each species was estimated to the nearest 1% in each of the 1-m^2 subplots. Species richness, measured at 1-, 10-, 100-, and 1000-m^2 spatial scales, included all vascular plants present as seedlings or mature plants that were rooted within each plot. Plant species names follow Hickman 1993 and Welsh et al. 1987.

Species richness was calculated as the number of higher vascular plant species at 4 spatial scales in each sampling plot (1, 10, 100, and 1000 m^2), which were collectively used as response variables in a 2-way multivariate analysis of variance (MANOVA) to evaluate effects of site, fire, and the site-by-fire interaction (Roy's greatest root test statistic; Sokal and Rohlf 1995). We similarly performed separate analyses for native, alien, woody perennial, herbaceous perennial, perennial grass, cacti, annual grass, and annual forb species richness. The list of species comprising each of these groups is in the Appendix. Raw data were used in these analyses, since they were normally distributed and homoscedastic. Significant effects for these and all other tests were considered at $P \leq 0.05$.

Species evenness was calculated as Pielou's J' (Ludwig and Reynolds 1988). These data were not normally distributed and transformations did not improve the data structure; therefore, the nonparametric median test was used to evaluate the significant effects of site, fire, and the site-by-fire interaction (Sokal and Rohlf 1995). Patterns of species evenness were also evaluated by visually inspecting the rank-order plots of species cover in burned and unburned areas at each study site.

Total cover, averaged from the ten 1-m^2 subplots within each sampling plot, was analyzed using analysis of variance (ANOVA) to evaluate effects of site, fire, and the site-by-fire interaction. Cover of aliens versus natives, individual alien species, and various plant life-forms was evaluated separately using MANOVA. Alien cover categories included *Bromus madritensis* ssp. *rubens*, *Bromus tectorum*, *Erodium cicutarium*, and other alien species. Life-form categories were woody perennials, herbaceous perennials, perennial grasses, cacti, annual grasses, and annual forbs. Cover data were arcsine transformed prior to analyses.

Frequency was calculated among the ten 1-m^2 subplots within each sampling plot, and ANOVA was used to evaluate effects of site, fire, and the site-by-fire interaction. Total alien frequency and frequency of alien annual grasses and *Erodium cicutarium* were analyzed separately, and data were untransformed.

RESULTS

Plant Diversity

UNBURNED BLACKBRUSH.—Species richness averaged 11, 20, 30, and 49 species at progressively larger spatial scales in unburned blackbrush (Fig. 1). Richness was much higher for natives (9, 17, 28, and 46 species) than aliens (2, 2, 2, and 3 species) and declined in order from annual forbs, woody perennials, herbaceous perennials, annual grasses, cacti, to perennial grasses (Table 1). Richness varied among sites ($F_{4,16} = 47.26$, $P < 0.0001$), and no single site had the highest richness at all 4 spatial scales. For example, the Spring Mountain site had the lowest richness at 1 m^2 but the highest at 1000 m^2.

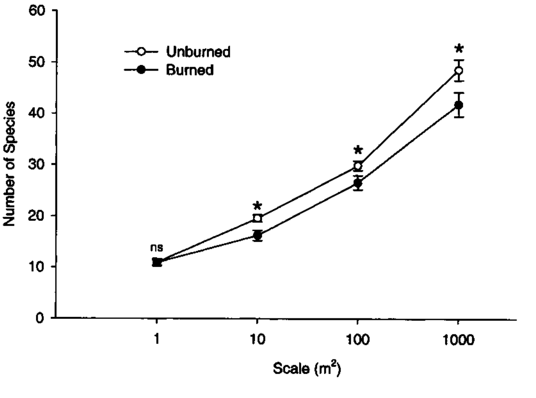

Fig. 1. Total species richness in unburned and burned blackbrush averaged over the 3 study sites. Asterisks indicate statistically significant ($P \leq 0.5$) differences between burned and unburned values at a given scale.

TABLE 1. Species richness of higher vascular plants at 4 spatial scales in unburned (U) and burned (B) blackbrush within each site, and among all sites combined, during spring 2001. Values are averages (±1 $s_{\bar{x}}$; $n = 4$ per site per fire history) and burn effects for each scale are indicated as not significant (ns), negative (- $P \le 0.05$, -- $P \le 0.01$, --- $P \le 0.001$), or positive (+ $P \le 0.05$, ++ $P \le 0.01$, +++ $P \le 0.001$); and significant across all scales (* $P \le 0.05$, ** $P \le 0.01$, *** $P \le 0.001$).

	1 m²			10 m²			100 m²			1000 m²		
	U	B		U	B		U	B		U	B	
ALL VASCULAR PLANTS												
Beaver Dam **	12.7 (0.28)	10.8 (0.49)	-	18.9 (0.46)	14.3 (0.93)	--	27.0 (0.89)	20.9 (0.38)	---	42.1 (2.45)	32.4 (1.34)	-
Joshua Tree ns	12.6 (0.30)	12.9 (0.24)	ns	21.9 (1.09)	20.4 (0.95)	ns	31.4 (1.55)	28.0 (1.08)	ns	47.9 (0.75)	43.6 (2.47)	ns
Spring Mt. ns	7.8 (0.57)	9.0 (0.30)	ns	18.0 (1.08)	14.0 (0.88)	ns	31.1 (1.66)	30.8 (1.75)	ns	55.8 (2.88)	49.5 (1.77)	ns
Sites combined **	11.0 (0.72)	10.9 (0.52)	ns	19.6 (0.70)	16.2 (1.01)	---	29.8 (0.95)	26.5 (1.40)	--	48.6 (2.05)	41.8 (2.36)	---
ALIENS												
Beaver Dam ns	2.9 (0.04)	3.0 (0.01)	ns	3.0 (0.00)	3.0 (0.00)	ns	3.0 (0.00)	3.0 (0.00)	ns	3.1 (0.13)	3.0 (0.00)	ns
Joshua Tree ns	1.2 (0.11)	1.8 (0.08)	++	1.8 (0.33)	2.1 (0.24)	ns	2.0 (0.35)	2.6 (0.13)	ns	2.9 (0.32)	3.8 (0.14)	+
Spring Mt. *	1.2 (0.07)	3.3 (0.19)	+++	1.6 (0.30)	4.1 (0.06)	+++	2.0 (0.29)	4.0 (0.00)	+++	2.8 (0.25)	4.3 (0.14)	++
Sites combined ***	1.8 (0.24)	2.7 (0.20)	+++	2.2 (0.23)	3.1 (0.25)	+++	2.3 (0.20)	3.2 (0.18)	+++	2.9 (0.14)	3.7 (0.17)	+++
NATIVES												
Beaver Dam **	9.7 (0.32)	7.8 (0.50)	-	15.9 (0.46)	11.3 (0.93)	--	24.0 (0.89)	17.9 (0.38)	---	39.0 (2.44)	29.4 (1.34)	-
Joshua Tree ns	11.3 (0.29)	11.1 (0.30)	ns	20.1 (0.86)	18.3 (0.73)	ns	29.4 (1.52)	25.4 (1.20)	ns	45.0 (0.89)	39.9 (2.40)	ns
Spring Mt. ns	6.6 (0.52)	5.7 (0.46)	ns	16.4 (0.83)	9.9 (0.94)	--	29.2 (1.49)	26.8 (1.75)	ns	53.0 (2.79)	45.3 (1.85)	ns
Sites combined ***	9.2 (0.63)	8.2 (0.71)	--	17.4 (0.68)	13.2 (1.19)	---	27.5 (1.02)	23.3 (1.34)	---	45.7 (2.08)	38.2 (2.23)	---
WOODY PERENNIALS												
Beaver Dam ns	1.5 (0.04)	1.3 (0.12)	ns	3.3 (0.47)	2.8 (0.45)	ns	6.3 (0.97)	5.4 (0.13)	ns	11.3 (1.42)	8.8 (0.78)	ns
Joshua Tree **	1.2 (0.02)	0.2 (0.07)	---	2.1 (0.16)	0.6 (0.13)	---	5.1 (0.66)	1.6 (0.13)	--	10.1 (0.55)	5.8 (0.63)	--
Spring Mt. ns	2.4 (0.16)	1.3 (0.13)	--	5.3 (0.33)	2.5 (0.37)	--	10.4 (0.66)	7.5 (0.54)	-	17.9 (0.88)	14.8 (0.52)	-
Sites combined ***	1.7 (0.16)	0.9 (0.17)	---	3.6 (0.44)	2.0 (0.34)	---	7.3 (0.79)	4.8 (0.75)	---	13.1 (1.16)	9.8 (1.18)	---
HERBACEOUS PERENNIALS												
Beaver Dam ns	1.2 (0.16)	1.0 (0.09)	ns	1.8 (0.20)	1.6 (0.28)	ns	3.0 (0.20)	2.8 (0.25)	ns	5.9 (0.47)	5.4 (0.24)	ns
Joshua Tree ns	0.4 (0.05)	0.3 (0.09)	ns	1.6 (0.22)	1.6 (0.30)	ns	2.6 (0.32)	2.1 (0.24)	ns	4.9 (0.52)	4.4 (0.24)	ns
Spring Mt. ns	0.5 (0.10)	1.1 (0.11)	++	1.8 (0.23)	1.4 (0.16)	ns	4.0 (0.74)	4.4 (0.75)	ns	9.0 (1.21)	7.4 (0.24)	ns
Sites combined ns	0.7 (0.11)	0.8 (0.11)	ns	1.7 (0.11)	1.5 (0.14)	ns	3.2 (0.30)	3.1 (0.38)	ns	6.6 (0.68)	5.7 (0.40)	ns

TABLE 1. Continued.

	1 m²		10 m²		100 m²		1000 m²	
	U	B	U	B	U	B	U	B
PERENNIAL GRASSES								
Beaver Dam *	0.1 (0.08)	0.2 (0.07) ns	0.2 (0.06)	0.1 (0.06) ns	0.3 (0.14)	0.9 (0.13) +	0.6 (0.32)	1.8 (0.25) +
Joshua Tree ns	0.3 (0.06)	0.3 (0.07) ns	1.3 (0.16)	0.8 (0.18) ns	1.9 (0.13)	2.1 (0.55) ns	2.6 (0.38)	3.6 (0.32) ns
Spring Mt. **	0.2 (0.04)	0.6 (0.06) ++	0.5 (0.27)	1.0 (0.18) ns	2.0 (0.20)	2.6 (0.32) ns	2.6 (0.38)	3.6 (0.13) +
Sites combined *	0.2 (0.04)	0.3 (0.06) +	0.7 (0.17)	0.6 (0.14) ns	1.4 (0.26)	1.9 (0.30) +	2.0 (0.34)	3.0 (0.30) +++
CACTI								
Beaver Dam ns	0.0 (0.00)	0.0 (0.00) ns	0.3 (0.19)	0.0 (0.00) ns	0.9 (0.31)	0.6 (0.24) ns	2.6 (0.72)	1.5 (0.41) ns
Joshua Tree **	0.0 (0.01)	0.0 (0.00) ns	0.0 (0.00)	0.0 (0.00) ns	0.8 (0.14)	0.0 (0.00) --	1.3 (0.14)	0.5 (0.20) -
Spring Mt. **	0.1 (0.03)	0.0 (0.01) -	0.3 (0.12)	0.0 (0.00) -	1.1 (0.24)	0.3 (0.30) -	3.4 (0.13)	1.1 (0.13) ---
Sites combined **	0.0 (0.02)	0.0 (0.00) --	0.2 (0.08)	0.0 (0.00) -	0.9 (0.14)	0.3 (0.13) --	2.4 (0.35)	1.0 (0.19) ---
ANNUAL GRASSES								
Beaver Dam *	3.3 (0.17)	3.1 (0.11) ns	3.8 (0.18)	3.4 (0.24) ns	4.0 (0.00)	3.4 (0.13) --	4.3 (0.14)	4.0 (0.20) ns
Joshua Tree ns	1.2 (0.11)	1.5 (0.12) ns	1.8 (0.31)	1.7 (0.06) ns	1.8 (0.48)	2.3 (0.25) ns	2.5 (0.35)	2.9 (0.24) ns
Spring Mt. **	1.1 (0.24)	2.0 (0.07) +++	1.6 (0.16)	2.4 (0.07) ++	1.6 (0.13)	2.3 (0.25) ns	2.4 (0.24)	3.3 (0.14) +
Sites combined *	1.9 (0.31)	2.2 (0.21) ++	2.4 (0.32)	2.5 (0.22) ns	2.5 (0.36)	2.6 (0.20) ns	3.0 (0.29)	3.4 (0.18) ns
ANNUAL FORBS								
Beaver Dam *	6.6 (0.32)	5.3 (0.32) -	9.6 (0.24)	6.6 (0.16) ---	12.6 (0.75)	7.9 (0.24) ---	17.5 (0.84)	11.0 (0.74) --
Joshua Tree ns	9.4 (0.28)	10.7 (0.40) +	15.1 (0.81)	15.7 (1.02) ns	19.3 (0.78)	19.9 (0.72) ns	26.3 (0.66)	26.5 (1.00) ns
Spring Mt. ns	3.5 (0.45)	4.2 (0.26) ns	8.5 (1.00)	6.8 (0.51) ns	12.0 (0.61)	13.8 (0.63) ns	20.5 (1.06)	19.5 (1.36) ns
Sites combined *	6.5 (0.75)	6.7 (0.88) ns	11.1 (0.96)	9.7 (1.33) -	14.6 (1.06)	13.8 (1.51) ns	21.4 (1.19)	19.0 (1.99) --

Species richness increased 446% between the 1- and 1000-m^2 spatial scales (Fig. 1), but the percent increase differed between natives (497%) and aliens (160%; Table 1). As a result, there was a decline in the percentage of alien species at progressively larger spatial scales (16%, 11%, 8%, and 6% alien species; Fig. 2). The percent increase in richness between 1- and 1000-m^2 scales also varied among plant life-forms: cacti (6000%), perennial grasses (1000%), herbaceous perennials (943%), woody perennials (771%), annual forbs (320%), and annual grasses (158%).

Species evenness in unburned blackbrush did not differ significantly among sites (χ^2 = 0.9583, P = 0.6193), due to the high dominance of *Coleogyne* cover at all sites (Fig. 3).

BURNED BLACKBRUSH.—Species richness in burned blackbrush was 20%, 10%, and 14% lower than in unburned blackbrush at the 10-, 100-, and 1000-m^2 spatial scales (Table 1). Richness did not decline significantly after fire at the 1-m^2 scale, except at the Beaver Dam site. The effects of burning on richness varied among sites (site-by-fire interaction, $F_{4,16}$ = 4.34, P = 0.0145) and was strongest at Beaver Dam (Table 1).

Effects of fire on species richness differed between aliens and natives and among plant life-forms. Alien richness increased, whereas native richness decreased, after fire (Table 1). Accordingly, the percentage of alien species increased after fire ($F_{4,15}$ = 28.40, P < 0.0001; Fig. 2). Richness of annual and perennial grasses increased, whereas richness of woody perennials and annual forbs diminished after burning (Table 1), but the responses of all life-forms varied among sites ($F_{5,15}$ = 5.98, P = 0.0031).

Burning extended evenness from 0.54 ± 0.04 (1 $s_{\bar{x}}$) in unburned to 0.65 ± 0.01 in burned plots, and the effect was strongest at Spring Mountain where there was a 56% increase. Fire enhanced species evenness by decreasing cover of *Coleogyne* and increasing the equitability of cover among other species (Fig. 3).

Plant Cover and Alien Frequency

Total plant cover in unburned blackbrush averaged 49% (46–51% range). *Coleogyne* was by far the most dominant plant species at 26% absolute cover, comprising 53% of total cover and 73% of woody perennial cover (Fig. 3).

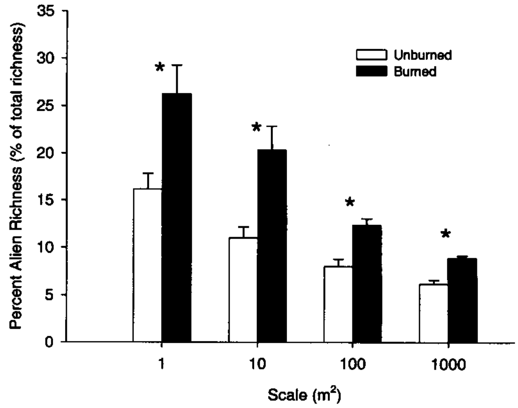

Fig. 2. Percent of total species richness comprising aliens in unburned and burned blackbrush. Asterisks indicate statistically significant ($P \le 0.5$) differences between burned and unburned values at a given scale.

Total cover in burned blackbrush was 50% (41–51% range), virtually the same as unburned blackbrush, but *Coleogyne* was almost completely removed by fire. In the absence of *Coleogyne*, a variety of species dominated the cover of burned areas. At Beaver Dam the burned area was dominated by *Erodium cicutarium*, *Gutierrezia sarothrae*, *Thamnosma montana*, *Astragalus nuttalianus* ssp. *imperfectus*, and *Bromus madritensis* ssp. *rubens* (Fig. 3a). At Joshua Tree the burned area was dominated by *Mentzelia affinis* and *Bromus tectorum*, followed by *Amsinckia tesselata*, *Chaenactis stevioides*, *Sphaeralcea ambigua*, *Erodium cicutarium*, and *Achnatherum speciosa* (Fig. 3b). At Spring Mountain, *Encelia virginensis*, *Erodium cicutarium* and *Baileya multiradiata* dominated the burned area, followed in abundance by *Prunus fasciculata*, *Gutierrezia sarothrae*, and *Bromus madritensis* ssp. *rubens* (Fig. 3c).

Although total cover returned to prefire levels 6–14 years postfire, patterns of recovery varied significantly among plant life-forms. Cover of woody perennials was 60% lower, and cover of all other plant life-forms was 170–450% higher, in burned than unburned blackbrush (Table 2). Annual forb cover increased 266% after burning, was higher than that of any other life-form in burned areas (21%), and increased significantly after burning at all 3 sites. Responses to fire by other plant life-forms varied among sites. Cover of annual grasses increased significantly only at

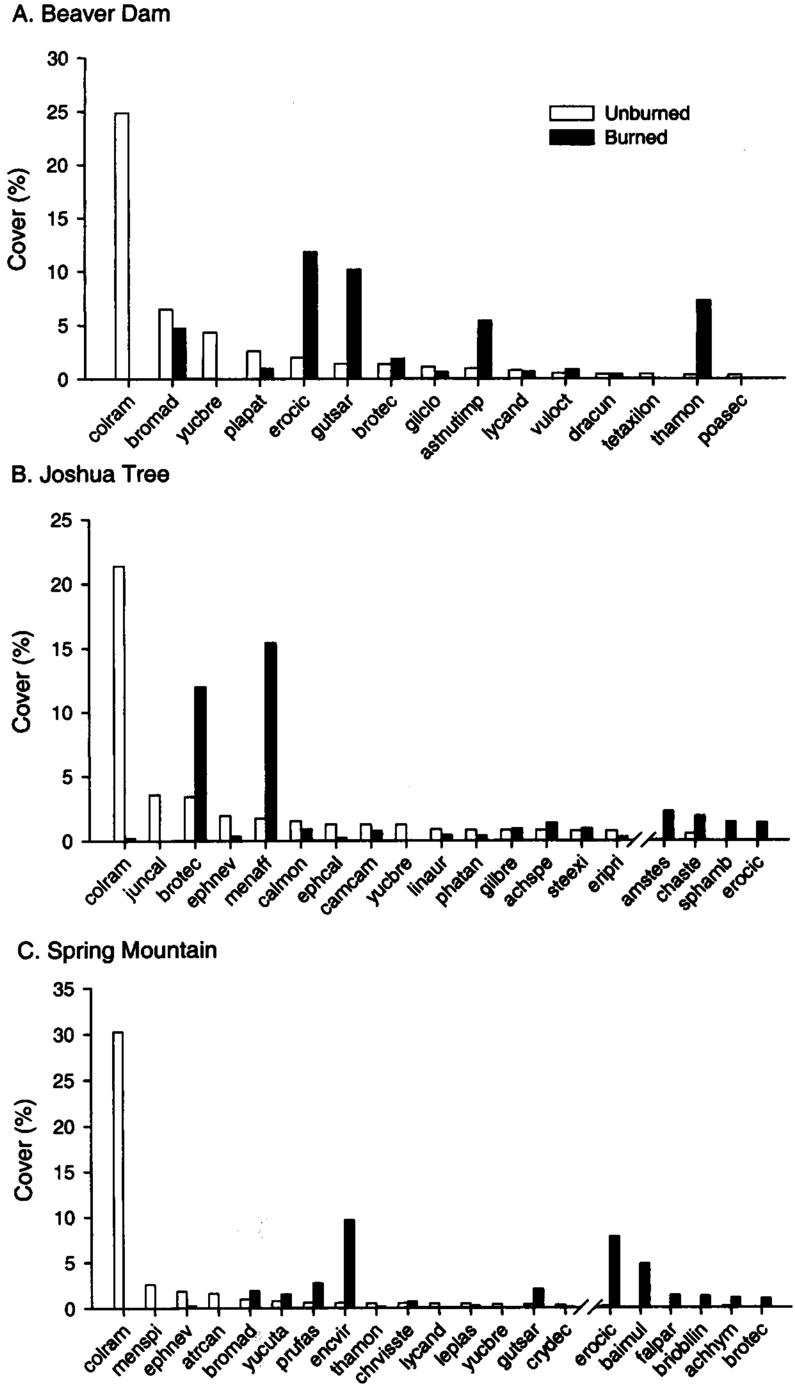

FIG. 3. Percent cover distribution of species in unburned and burned blackbrush. Species were arranged along the abscissa in their rank order of cover dominance in the unburned plots. Additional species were added to the right of an axis break if any of the top 15 species in burned plots were not among those plotted for the unburned plots. Species codes are listed in the Appendix.

TABLE 2. Percent cover of higher vascular plants in unburned (U) and burned (B) blackbrush within each study site, and among all sites combined, during spring 2001. Values are averages (±1 $s_{\bar{x}}$; n = 4 per site per fire history) and burn effects for each group are indicated as not significant (ns), negative (- $P \le 0.05$, -- $P \le 0.01$, --- $P \le 0.001$), or positive (+ $P \le 0.05$, ++ $P \le 0.01$, +++ $P \le 0.001$); and significant across all groups (* $P \le 0.05$, ** $P \le 0.01$, *** $P \le 0.001$).

	Alien species							
	Bromus madritensis rubens		*Bromus tectorum*		*Erodium cicutarium*		Others	
	U	B	U	B	U	B	U	B
Beaver Dam **	6.5 (2.24)	4.7 (0.22) ns	1.4 (0.29)	1.9 (0.36) ns	2.0 (0.20)	11.8 (3.48) ++	0.0 (0.00)	0.0 (0.00) ns
Joshua Tree ns	0.4 (0.18)	0.8 (0.34) ns	3.4 (0.63)	12.0 (2.10) ++	0.0 (0.01)	1.4 (1.06) ns	0.3 (0.18)	0.3 (0.08) ns
Spring Mt. **	1.0 (0.11)	1.9 (0.17) ++	0.0 (0.01)	1.0 (0.11) +++	0.2 (0.08)	7.8 (2.38) ++	0.0 (0.03)	0.6 (0.13) ++
Sites combined ***	2.6 (1.07)	2.5 (0.51) ns	1.6 (0.48)	5.0 (1.63) +++	0.7 (0.28)	7.0 (1.84) +++	0.1 (0.07)	0.3 (0.09) ++

	Life-forms[a]									
	Woody perennials		Herbaceous perennials		Perennial grasses		Annual grasses		Annual forbs	
	U	B	U	B	U	B	U	B	U	B
Beaver Dam ns	32.4 (2.94)	20.5 (3.73) -	0.7 (0.09)	0.7 (0.11) ns	0.4 (0.33)	0.1 (0.08) ns	8.7 (2.44)	7.7 (0.58) ns	8.6 (0.34)	20.2 (4.10) +
Joshua Tree *	30.6 (4.15)	1.9 (0.86) ---	0.7 (0.22)	2.1 (0.91) ns	1.0 (0.31)	2.3 (0.54) ns	4.1 (0.65)	13.1 (2.21) ++	12.9 (1.18)	31.2 (3.66) ++
Spring Mt. *	41.4 (1.57)	19.4 (3.72) --	0.3 (0.05)	5.2 (0.99) +++	0.3 (0.13)	1.9 (0.64) +	1.0 (0.10)	3.0 (0.22) +++	2.2 (0.28)	11.5 (1.99) +++
Sites combined ***	34.8 (3.04)	13.9 (3.04) ---	0.6 (0.09)	2.7 (0.70) +++	0.6 (0.17)	1.5 (0.38) +	4.6 (1.22)	7.9 (1.42) +++	7.9 (1.38)	21.0 (3.00) +++

[a]Cacti are excluded because of minimal cover and no statistically significant differences.

Joshua Tree and Spring Mountain, and cover of herbaceous perennials and perennial grasses increased significantly only at Spring Mountain.

Fire boosted cover of aliens 191% ($F_{1,18}$ = 32.22, P < 0.0001) and reduced cover of natives 26% ($F_{1,18}$ = 16.15, P = 0.0008; Fig. 4), and these trends did not differ significantly among sites ($F_{2,18}$ = 0.13, P = 0.74). As a result, the proportion of total cover comprising aliens increased from 10% before fire to 31% after fire ($F_{1,18}$ = 38.22, P < 0.0001).

Alien plant species that increased the most in cover differed significantly among sites ($F_{4,16}$ = 4.33, P = 0.0146). At Beaver Dam and Spring Mountain the enhanced alien cover was mainly due to *Erodium cicutarium*, whereas at Joshua Tree the increase was mainly caused by *Bromus tectorum* (Table 2). Cover of the relatively uncommon alien species *Salsola tragus*, *Bromus trinii*, and *Schismus* spp. collectively increased after fire, due to their strong positive response at the Spring Mountain site. *Bromus madritensis* ssp. *rubens* cover exhibited a slight increase at Spring Mountain, but the overall effect of fire across all sites was not significant.

Total frequency of aliens did not increase significantly due to fire ($F_{1,18}$ = 1.57, P = 0.2266), but there was a significant site-by-fire effect ($F_{2,18}$ = 4.01, P = 0.0363), and alien frequency did increase significantly from 54% to 78% at Spring Mountain ($F_{1,6}$ = 14.99, P < 0.0083). Responses varied among alien species, with *Erodium cicutarium* exhibiting the greatest increase in frequency, from 37% in unburned to 67% in burned areas ($F_{1,18}$ = 30.69, P <0.0001). The response of *Erodium cicutarium* frequency to burning varied among sites ($F_{2,18}$ = 10.44, P = 0.0010), increasing from 1% to 29% at Joshua Tree ($F_{1,6}$ = 5.22, P = 0.0623), 13% to 75% at Spring Mountain ($F_{1,6}$ = 32.89, P = 0.0012), and 96% to 98% at Beaver Dam ($F_{1,6}$ = 0.20, P = 0.6704). The overall combined frequency of the alien annual grasses *Bromus madritensis* ssp. *rubens* and *Bromus tectorum* did not differ significantly ($F_{1,18}$ = 0.79, P < 0.4410) between unburned 79% (±7) and burned 84% (±5) areas.

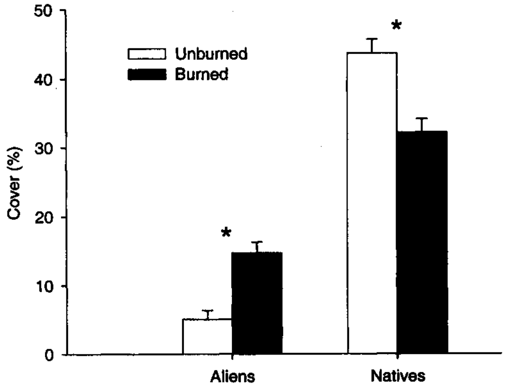

Fig. 4. Percent cover of alien and native species in unburned and burned blackbrush. Alien and native species are listed in the Appendix. Asterisks indicate statistically significant ($P \leq 0.5$) differences between burned and unburned values for aliens or natives.

DISCUSSION

Species Richness in Unburned Blackbrush

Results from our 3 study sites suggest that species richness in unburned Mojave Desert blackbrush is not lower than other vegetation types in western North America, as we had predicted it would be. In the current study we reported 11 total plant species per 1 m^2, which is comparable to 7 species per 1 m^2 reported in ponderosa pine and shortgrass steppe, 8 in tallgrass prairie, 9 in aspen, and 12 in mixed grasslands (Stohlgren et al. 1999a). We reported an average of 7 woody perennial species per 100 m^2 (10 at Spring Mountain), which compares closely with 6 woody perennial species per 100 m^2 reported in pinyon/juniper/sagebrush, 8 in creosote bush/bursage, and 8–10 reported for unburned blackbrush near our Spring Mountain study site (Lei and Walker 1995). We reported 47 total species per 1000 m^2, compared to 38 species per 1000 m^2 in chaparral (Schluter and Ricklefs 1993), 45 species in the Colorado Rocky Mountains (Stohlgren et al. 1999a), 50 species in Mediterranean regions with rainfall similar to the sites in the current study (150 mm; Rosenzweig and Abramsky 1993), and 65–70 species in semiarid grasslands and shrublands (Schluter and Ricklefs 1993). We also reported 46 native species and 3 alien species per 1000 m^2, which compared favorably with 32 native species and 3 alien species in Rocky Mountain grasslands (Stohlgren et al. 1999b). Thus, species richness of all higher vascular plants, woody perennial species, and alien species at our Mojave Desert blackbrush sites was comparable to other major vegetation types.

Species richness increased logarithmically between the 1- and 1000-m^2 scales, but this increase was much higher for natives than aliens. This pattern suggests that native richness was more closely related to increased environmental heterogeneity at successively larger spatial scales. Apparently, the spatial distribution of the few alien species in this study was influenced more by environmental heterogeneity at the smaller scales, whereas distribution of the many native species was affected more equitably by heterogeneity at all scales. The greater richness at higher spatial scales also varied among plant life-forms. Perennials increased proportionally more than annuals, indicating that the former were responding more to environmental variation at successively higher spatial scales. Heterogeneity at 1 m^2 was due to the shrub-intershrub gradient, and at 1000 m^2 it was due to the microtopographic gradient from finer-textured soils of rainfall runoff areas (hummocks) to coarser-textured soils of run-on areas (washlets; Brooks 1999). These results demonstrate that different spatial scales can produce different relative estimates of species richness between natives and aliens, and among plant life-forms in blackbrush.

Species evenness in unburned blackbrush appeared to be low, with *Coleogyne* dominating that landscape. However, comparisons with values from other studies were confounded by a wide range of evenness metrics and sampling designs, or insufficient published descriptions of the methods that we used. As a result, we were unable to include any reliable comparisons in this paper.

The single year of plant community data reported in this study should be sufficient to evaluate general diversity patterns in blackbrush. Winter rainfall from October through March ranged from 88% to 111% of the 30-year average at the study sites, resulting in a moderately diverse display of native annuals (MLB personal observation). These rainfall estimates are based on data from the closest weather stations to each site that had the necessary weather data for calculating 30-year averages (1 to 3 stations per site; National Climatic Data Center). There may have been some annual plant species that remained dormant as seeds and were not detected, but this would only have caused species richness to be underestimated and would not have affected the conclusion that species richness at our 3 Mojave Desert blackbrush sites was comparable to other vegetation types.

Effects of Fire on Blackbrush Community Structure

Fire removed virtually all *Coleogyne* cover, which is consistent with most other reports (Jenson et al. 1960, Bowns 1973, Beatley 1976, Callison et al. 1985, West and Young 2000). The loss of *Coleogyne* as the single dominant species, and its replacement by 2 to 5 other co-dominant species 6–14 years postfire, resulted in increased species evenness but decreased species richness. Decreased richness after *Coleogyne* removal and the finding that species richness in blackbrush was similar to other vegetation types were inconsistent with the assertion that *Coleogyne* has a strong negative effect on the number of other coexisting species (Bowns 1973, Beatley 1976, Bowns and West 1976). Thus, the cover dominance of *Coleogyne* may not prevent the coexistence of a wide range of other plant species.

Loss of *Coleogyne* cover is not the only effect of fire and therefore not the only potential factor related to postfire plant community patterns. Fire also can kill mature plants and seeds and alter soil characteristics (Whelan 1995). It is likely that many native plant species recover slowly after blackbrush fires because they evolved in a desert ecosystem where fire is infrequent. Reduced species richness 6–14 years postfire may result from slow recovery of these native species, especially woody perennials.

Alien species are often invasive, responding rapidly to increased availability of limiting resources created by disturbances such as fire (Grime 1977, Chapin et al. 1986). It is therefore not surprising that fire increased alien richness and cover in this study, as we predicted it would. The single site where alien richness and cover of either *Bromus tectorum* or *B. madritensis* ssp. *rubens* did not increase significantly after fire was Beaver Dam, where moderate levels of past and current cattle grazing may have allowed aliens to establish relatively high levels of richness and annual grass cover in unburned blackbrush. The other 2 sites had not been grazed by livestock for many decades and had much lower levels of alien richness and cover. These results suggest that relatively undisturbed blackbrush may be somewhat resistant to invasion by alien species, and the effects of fire on previously disturbed blackbrush may not modify dominance of alien annual plants if disturbance levels are already high.

Although alien richness and cover were consistently higher in burned than unburned blackbrush, no single alien plant life-form or species dominated all sites. Alien annual grass cover increased the most after fire at Joshua Tree, whereas the alien annual forb *Erodium cicutarium* increased the most at the other 2 sites. Frequency of alien annual grasses did not differ between burned and unburned areas, indicating that the continuity of annual grass fuels was not affected by burning 6–14 years postfire. These results do not support the conclusions of others that alien annual grasses are typically among the most dominant postfire species in burned blackbrush (Jenson et al. 1960, West 1983, Callison et al. 1985) and that their heightened dominance after fire may increase landscape flammability (Holmgren 1960). However, these results are from a single year of annual plant sampling and must be interpreted cautiously.

Annual plant cover can vary dramatically among years of contrasting rainfall, especially for alien species in the Mojave Desert (Brooks 1999, 2000). Before plants were sampled in the current study, 2 of the previous 3 winter rainfall seasons experienced less than half of the long-term average rainfall in the Mojave Desert. In 1999 rainfall ranged from 16% to 54%, in 2000 it was 30% to 68%, and in 2001 rainfall averaged 88% to 111% of the 30-year average at rainfall stations near the 3 study sites (1 to 3 stations per site; National Climatic Data Center). It is probable that the seed bank of alien annual grasses, *Bromus* spp. in particular (Brooks 2000), was depleted during this drought. The dominance of alien annual grasses reported in the current study was therefore on the low end of the interannual range. It is likely that a few years of high rainfall would increase cover, and possibly frequency, of alien annual grasses, thus increasing landscape flammability (Rogers and Vint 1987, Schmid and Rogers 1988, Brooks 1999).

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APPENDIX. Higher vascular plant species sampled in unburned (U) and burned (B) blackbrush within each study site during spring 2001 (x = present). Nomenclature follows Hickman (1999) and Welsh et al. (1987).

		Beaver Dam		Joshua Tree		Spring Mt.	
	Code	U	B	U	B	U	B
ALIENS							
Annual grasses							
Bromus madritensis ssp. *rubens*	bromad	x	x	x	x	x	x
Bromus tectorum	brotec	x	x	x	x	x	x
Bromus trinii		x					
Schismus arabicus				x	x		
Schismus barbatus							x
Annual forbs							
Erodium cicutarium	erocic	x	x	x	x	x	x
Salsola tragus						x	x
NATIVES							
Woody perennials							
Acamptopappus spherocephalus		x		x	x	x	x
Ambrosia eriocentra							x
Artemisia dracunculus							x
Artemisia tridentata						x	
Atriplex canescens	atrcan					x	
Chrysothamnus nauseosus		x	x				x
Chrysothamnus paniculatus							x
Chrysothamnus viscidiflorus var. *stenophyllus*	chrvisste	x	x			x	x
Coleogyne ramosissima	colram	x	x	x	x	x	x
Coleogyne ramosissima (seedling)			x	x	x	x	x
Encelia virginensis	encvir	x	x			x	x
Ephedra californica	ephcal			x	x	x	x
Ephedra nevadensis	ephnev	x	x	x	x	x	x
Ephedra torreyana		x					
Ephedra viridis		x	x			x	x
Eriogonum fasciculatum var. *polifolium*				x	x	x	
Fallugia paradoxa	falpar						x
Grayia spinosa		x		x			
Gutierrezia sarothrae	gutsar	x	x	x		x	x
Hymenoclea salsola		x		x		x	x
Juniperus californicus	juncal			x	x		
Juniperus osteosperma						x	x
Krascheninnikovia lanata		x				x	x
Lycium andersonii	lycand	x	x	x	x	x	x
Lycium cooperi				x	x	x	x
Menodora spinescens	menspi					x	
Pinus monophylla						x	
Prunus fasciculatus	prufas	x	x			x	x
Psilostrophe cooperi			x				
Purshia mexicana var. *stansburyana*		x				x	x
Purshia tridentata var. *glandulosa*						x	x
Salazaria mexicana				x	x		
Salvia dorrii				x	x	x	x
Symphoricarpos longiflorus						x	
Tetradymia axillaris var. *longispina*		x		x		x	
Thamnosma montana	thamon	x	x			x	x
Thermophylla pentachaeta var. *belenidium*							x
Viguiera parishii						x	x
Yucca brevifolia	yucbre	x	x	x	x	x	x
Yucca utahensis	yucuta	x	x			x	x

APPENDIX. Continued.

	Code	Beaver Dam		Joshua Tree		Spring Mt.	
		U	B	U	B	U	B
Herbaceous perennials							
Arabis pulchra		x		x		x	x
Astragalus bernardianus				x	x		
Astragalus lentiginosus							x
Baileya multiradiata	bailmul	x				x	x
Calochortus flexuosus		x	x			x	x
Calochortus kennedyi				x			
Castilleja angustifolia		x				x	x
Caulanthus crassicaulis						x	x
Chamaesyce albomarginata				x	x		
Chamaesyce fendleri						x	x
Chenopodium incanum						x	
Cymopterus multinervatus		x	x				
Delphinium nuttalianum		x	x				
Delphinium parishii				x	x	x	x
Dichelostemma capitata		x	x	x	x		
Eriogonum inflatum							x
Eriogonum plumatella				x	x		
Erioneuron pulchellum			x			x	x
Gaura coccinea			x				
Lepidium fremontii		x	x			x	
Linum lewisii							x
Lomatium mohavense				x			
Lomatium nevadense						x	
Mirabilis bigelovii				x	x		
Mirabilis multiflorus		x	x				
Oenothera californica					x		
Penstemon palmeri							x
Penstemon sp.						x	
Phlox longifolia		x	x				
Phoradendron juniperinum				x			
Prenanthella exigua						x	x
Senecio multilobatus						x	x
Sphaeralcea ambigua	sphamb	x	x	x	x	x	x
Stephanomeria pauciflora						x	x
Streptanthus cordatus			x			x	
Tricardia watsonii		x					
Perennial grasses							
Achnatherum hymenoides	achhym	x		x	x	x	x
Achnatherum speciosum	achspe		x	x	x	x	x
Aristida purpurea			x			x	x
Elymus elymoides			x	x	x	x	x
Pleuraphis rigida				x	x		x
Poa secunda	poasec	x	x	x	x		
Cacti							
Echinocerus engelmanii		x	x	x		x	
Echinocerus triglochidiatus						x	
Escobaria vivipara desertii						x	x
Opuntia acanthocarpa		x	x				
Opuntia basilaris		x		x	x	x	x
Opuntia echinocarpa				x	x	x	
Opuntia erinacea		x	x				
Opuntia seedling							x
Annual grasses							
Poa bigelovii		x	x				
Poa unknown 1 (annual)				x			
Vulpia microstachys		x	x				
Vulpia octoflora	vuloct	x	x			x	x
Annual forbs							
Amsinckia tesellata	amstes	x	x	x	x		
Anisocoma acaulis				x			

APPENDIX. Continued.

	Code	Beaver Dam		Joshua Tree		Spring Mt.	
		U	B	U	B	U	B
Asteraceae unknown				x			
Asteraceae unknown 1 (annual)							x
Astragalus nuttalianus var. *imperfectus*	astnutimp	x	x				
Baileya pleniradiata		x	x				
Brickellia oblongifolia linoides	briobllin					x	x
Calyptridium monandrum	calmon			x	x		
Camissonia campestris	camcam			x	x	x	x
Camissonia unknown species 1					x		
Camissonia unknown species 2				x			
Centrostegia thurberi				x	x		
Chaenactis fremontii			x				
Chaenactis stevioides	chaste			x	x		
Cirsium neomexicanum							x
Claytonia perfoliata		x					
Coreopsis bigelovii					x		
Cryptantha circumcissa				x	x	x	x
Cryptantha decipiens	crydec	x	x		x	x	x
Cryptantha micrantha				x	x		
Cryptantha nevadensis						x	x
Cryptantha pterocarya		x	x	x	x	x	x
Cryptantha recurvata						x	x
Descurainia pinnata		x	x	x	x	x	x
Draba cuneatus	dracun	x	x			x	x
Eriastrum diffusum				x	x	x	
Erigeron divergens		x	x			x	x
Eriogonum annual unknown 1				x	x		
Eriogonum annual unknown 2				x	x		
Eriogonum annual unknown 1		x					
Eriogonum nidularium						x	x
Eriogonum pusillum						x	x
Eriogonum reniforme				x			
Eriophyllum pringlei	eripri			x	x		
Eriophyllum wallacei		x		x	x		
Eschscholzia minutiflora		x				x	
Filago depressum					x		
Gilia brecciarum ssp. *brecciarum*	gilbre			x	x		
Gilia clokeyi	gilclo	x	x			x	x
Ipomopsis polycladon						x	x
Langloisia setossisima		x			x	x	x
Lappula redowski						x	x
Layia glandulosa				x	x		
Lepidium lasiocarpum	leplas	x	x			x	x
Lesquerella tenella		x	x				
Linanthus aureus	linaur			x	x		x
Linanthus bigelovii		x		x	x		x
Linanthus demissus		x				x	x
Loeseliastrum schottii				x	x		
Macheranthera canescens						x	x
Macheranthera canescens var. *leucanthemifolia*			x				
Malacothrix glabrata		x		x	x		
Mentzelia affinis	menaff			x	x	x	x
Mentzelia nitens				x	x		x
Mimulus bigelovii				x	x	x	x
Monoptilon belloides		x					
Nama demissum				x	x	x	x
Nenacladus glanduliferus						x	x
Nemacladus longiflorus var. *breviflorus*		x		x	x		x
Nemophila menziesii				x	x		

APPENDIX. Continued.

	Code	Beaver Dam		Joshua Tree		Spring Mt.	
		U	B	U	B	U	B
Nyctaginaceae unknown 1					x		
Oenothera deltoides						x	x
Oxytheca perfoliata						x	
Oxytheca trilobata					x		
Pectocarya platycarpa					x		
Phacelia distans							x
Phacelia fremontii		x	x			x	x
Phacelia tanacetifolia	phatan			x	x		
Phacelia vallis-mortae		x	x			x	
Plantago patagonica	plapat	x	x			x	x
Rafinesquia neomexicana			x	x	x		
Salvia columbariae				x	x		
Silene antirrhina		x	x				
Stephanomeria exigua	steexi		x	x	x	x	
Streptanthella longirostris		x				x	x
Syntricopappus fremontii		x	x				
Unknown species 2		x					
Uropappus lindleyi		x		x			
Vicia ludoviciana		x	x				
Yabea microcarpa		x					